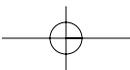
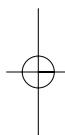
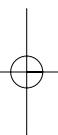
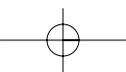
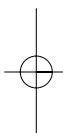
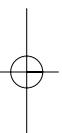
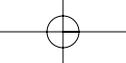


PART ONE

Introduction





CHAPTER ONE

Evolving Perspectives on Anthropoidea

Callum F. Ross and Richard F. Kay

The history of Anthropoidea is the history of primatology in a microcosm. Anthropoidea, Order Primates, Semiorder Haplorhini, Suborder, Anthropoidea is a particularly useful lens through which to focus on the history of primatology because from its roots in pre-evolutionary classifications, through its polyphyletic status under Simpsonian systematics, to its current conception as a monophyletic group, Anthropoidea has persisted as a “natural” group with relatively stable content. This essay examines how this common content has been imbued with different meanings by changing conceptions of classification and explanation in biology. In addition, just as studies of anthropoid phylogeny provide insight into extant anthropoids themselves, this essay aims to provide insight into the roots of current ideas about anthropoid origins. Thus, this brief survey provides historical background, placing the work of our colleagues in historical perspective, and examines the foundations of what we believe about anthropoid evolution today.

ESSENTIALISM

Anthropoidea was recognized as a natural group at the birth of modern classification. Linnaeus (Caroli a Linné) (1707–1778) classified *Simia* (monkeys

Callum F. Ross • Anatomical Sciences, Stony Brook University, Stony Brook NY 11794-8081
Richard F. Kay • Biological Anthropology and Anatomy, Duke University, Durham NC 27710

and apes) as one of four divisions of his first mammalian order Primates (animals with four parallel upper incisors and two pectoral mammae), the others being Homo (humans and orangutans), Lemur (lemurs, lorises, and flying lemurs), and Vespertilio (bats). Simia were primates with four incisors in each jaw, approximating one another in the midline; long foliate (or spear-shaped) canines separated from the incisors by a diastema; and blunt molars (Linnaeus, 1766, p. 54). They consisted of 35 species (e.g., pithecia, rosalia, oedipus, jacchus, midas, apella, capucina from South America), each of which was accompanied by a description of the characters distinguishing it from other species and by notes on its location.

As an essentialist, Linnaeus believed that what was natural about this classification were the unchanging, ideal essences of the genera (see Greene, 1959). The essences and categories existed the way they did because that was how God had created them. Consequently, no materialistic explanations were required, either for the existence of the essences, or for the categories they defined. In capturing and defining God's order, the very act of classifying constituted explanation enough.

RATIONALISM

E. Geoffroy Saint-Hilaire's and George Cuvier's classifications of animals, including Primates, attempted to ground classification on a rational foundation. Like Linnaeus, they believed that God had created animals, so a materialistic explanation for the existence of the categories was not necessary. However, they assumed that God used rational principles in creating animals and that the way to uncover God's plan was to apply rational principles to classification (Appel, 1987).

Geoffroy and Cuvier's (1795) collaborative classification of mammals was based on the rational principle of "subordination of characters," under which the subordination of categories in the classification was determined by the subordination of functions in organisms. The primary taxonomic divisions were based on those functions deemed to be most important in an animal's life, while secondary divisions were based on subordinate functions. Applying this principle, their first division of the Class Mammalia was based on the anatomy of the organs of generation and circulation, the second division on the anatomy of the tegument of the digits, the organs of tactile sense, and the third on the teeth, the organs of nutrition (Geoffroy and Cuvier, 1795). Accordingly, Quadrumanes, or Primates,

were defined as mammals because they gave birth to live young and nourished them with breasts, as members of the third embranchement because they had nails or claws (rather than flippers like marine mammals, or hooves like ungulates); and members of an unnamed group possessing three kinds of teeth. Quadrumanes were differentiated from all other mammals by possession of an opposable pollex and hallux. Within Quadrumanes, the genus Singes (anthropoids) was defined as those animals with four incisors in each jaw which were not procumbent and elongated as in lemurs and lorises (Geoffroy and Cuvier, 1795).

Geoffroy's and Cuvier's ideas about the principles underlying classification later diverged (Appel, 1987), and although this had little impact on the structure of the classifications, it did profoundly alter their meaning. In *Le Règne Animal*, Cuvier (1817) delineated the principle of "conditions of existence": the component parts of each animal must function together so that the animal survives successfully in its environment. Cuvier believed that when God created animals, He gave them forms that enabled them to function in their environment. Therefore, to construct a classification that recreated the natural system, and thereby to understand the works of the Creator, one had to use the structures that were used by animals to function in their environment. Thus, in a teleological sense, Cuvier provided a functional explanation for the structure of organisms, and by extension, also their natural groupings.

In accordance with these principles, Cuvier defined Singes—which had been elevated to familial rank by discoveries of new species—as:

Quadrumana with four straight incisors to each jaw, and flat nails to all the extremities—two characters which approximate them more nearly to Man than the subsequent genera. Their molars have also blunt tubercles like ours, and they subsist mainly on fruits; but their canines, being longer than the other teeth, supply them with a weapon which we do not possess, and require a vacant space in the opposite jaw to receive them when the mouth is closed (Cuvier, 1817, p. 42).

In contrast, Geoffroy rejected the Cuvierian notion that function restricted the form that God gave to animals, and instead argued that the form that animals were given determined the functions that they might perform. His studies of primates had convinced him that there were many intermediate forms that did not fit neatly into contemporary classifications. *Daubentonia*, for example, did not fit neatly into the orders of mammals, showing affinities with rodents, monkeys, makis (lemurs), and marsupials (Geoffroy, 1795). Moreover,

upon splitting Linnaeus' genus *Lemur* into five separate genera, *Lemur*, *Indri*, *Loris*, *Galago*, and *Tarsius*, Geoffroy argued that *Indri* was an intermediate between monkeys and makis, and that galagos were intermediates between lorises and *Tarsius* (Geoffroy, 1796). He cited these intermediate forms, and others among fishes, birds, and mammals, as evidence that transformations of "the same" organs could be traced through all vertebrates (and later all invertebrates too), and that all animals must therefore be formed on a single ideal plan (1818). This underlying plan unified diverse forms in nature.

Geoffroy's (1812a, 1812b) classification is close to our present conceptions of primate classification, is based on many of the features that we still use to divide up the order, and coins several higher taxonomic names still in use today. The Order Quadrumanes is defined by possession of a spherical braincase, a post-orbital bar separating the orbit from the tempora fossa, development of some agent of prehension, and possession of an opposable first digit, the latter being the most indicative character of the order. The order is divided into two families: Lemuriens, or Strepsirrhini (*Indri*, *Lemur*, *Lemur volans* [*Cynocephalus*], *Lemur pilodactylus* [*Daubentonia*], *Loris*, *Nycticebus*, *Galago*, *Tarsius*) and Singes (monkeys or anthropoids). Singes comprises Catarrhini, or Old World monkeys and apes; and Platyrrhini, or American monkeys, consisting of three groups, roughly approximating callitrichines, atelines, and pitheciines.

Despite their divergent views on the meaning of classification, Cuvier and Geoffroy both recognized, as Linnaeus had, that anthropoids (*Simia* or Singes) were fundamentally different from prosimians (*Lemur* of Linnaeus, Strepsirrhini of Geoffroy, 1812b; makis of Cuvier, 1817). Explanations for the existence of the features used to group these animals (and therefore for the existence of the groups as a whole) resided in the principles on which the classifications were based. These principles were primarily those hypothesized to have guided God in creating animals, so any explanations for the existence of biological structures were in the end teleological, and, in the case of Geoffroy, idealistic as well. However, in important respects, Geoffroy and Cuvier pointed the way toward future materialistic explanations for biological phenomena. Geoffroy's notion of a common plan underlying all vertebrates, manifesting itself through ideal transformations from one form to another, could easily become a notion of evolution by interpreting the transformations as actual rather than ideal events. In this context, Cuvier's notion that functional requirements determine organismal form could become a mechanism for guiding modification during descent. The work of Geoffroy and Cuvier contained the seeds of a materialistic explanation for evolution.

PARALLELISM

The publication of Darwin's *The Origin of Species* in 1859 might have spurred biologists to classify organisms on the basis of evolutionary relationships. However, skepticism about the possibility of reconstructing phylogeny and a belief that the "laws of evolution" required a high degree of polyphyly (Huxley [1880] in Simpson, 1961, p. 120) made workers avoid phylogenetic considerations in classification. Thus, T. H. Huxley (1863) classified primates into "seven families of about equal systematic value" which were not related to each other evolutionarily: Anthropini (*Homo sapiens*), Catarhini, Platyrrhini (non-marmoset ceboids), Arctopithecini (marmosets), Lemurini, Cheiromyini (*Daubentonia*), and Galeopithecini.

Similarly, functional or adaptive explanations for the existence of groups might have been expected in light of Darwin's emphasis on the importance of adaptation in evolution. However, for a number of reasons this did not happen. In general, the study of function was the purview of physiology, not of post-Darwinian 19th century comparative anatomy (Cole, 1975; Russell, 1982). More specifically, and more importantly for the subsequent study of primate evolution, at the end of the 19th century, there was no adequate theory for the origin and inheritance of variation, and both blending inheritance and soft inheritance (inheritance of acquired characters) were still widely accepted (Mayr, 1982). Soft inheritance made it easy to accept orthogenesis as the explanation for the long-term trends seen in the fossil record (e.g., Osborn, 1889, 1895, 1902) and made parallelism seem pervasive. Different lineages subject to the same external forces would evolve the same features in parallel. The lack of an adequate theory of inheritance, combined with the paleontological evidence for long-term evolutionary trends, led many workers to believe that parallelism and orthogenesis were pervasive and important phenomena in evolution.

This belief impacted the future study of primate evolution through the theories of St. George Jackson Mivart and Henry Fairfield Osborn, instrumental figures in shaping primatology at the beginning of the 20th century (Cartmill, 1982). Mivart believed that natural selection is incapable of explaining instances of parallelism and convergence. He attributed these phenomena to a "latent tendency" within organisms for sudden large-scale variation that is stimulated into "action by the stimulus of external conditions," but which is channeled by "an internal law [which] presides over the actions of every part of every individual, and of every organism as a unit, and of the entire organic world as a whole" (1871, p. 255). Osborn rejected natural selection as the

primary mechanism of evolution because it failed to explain how variations appropriate to the problems faced by organisms appeared in populations, and why, when such variations arose in some individuals, they were not bred out of the population by blending inheritance (Osborn, 1889, 1895). To explain parallelism and convergence, Osborn advanced his principle that “definite tendencies in variation spring from very remote ancestral causes” (Osborn, 1895, pp. 433–434), a principle he referred to as the *Law of Latent or Potential Homology* (1902) and which was succinctly expressed in the aphorism “the *same* results appear independently in descendants of the *same* ancestors” (Osborn [1908] quoted in Elliot Smith, 1919).

Mivart and Osborn’s belief in pervasive parallelism fueled by innate tendencies to vary in certain directions influenced early 20th century perceptions of the problems of primate evolution and classification in three ways.

First, it made polyphyletic taxa acceptable in primate classification. For example, Mivart believed that Anthroidea (Mivart, 1864)—humans, apes, and all monkeys—and Lemuroidea should be classified together as Primates even though he thought they arose separately from nonprimate ancestors. Moreover, he also thought that New and Old World anthropoids were descended from an ancestral stock that was not recognizably primate, let alone anthropoid (Mivart, 1873). The interpretation of Anthroidea as a polyphyletic taxon was facilitated by observations that New and Old World anthropoids exhibit obvious differences in form (Flowers, 1866; Mivart, 1874), and were situated on two widely separate continents. Possible fossil ancestors of these two groups recovered on both sides of the Atlantic provided apparent support for the notion of anthropoid diphyle. *Omomyx* (Leidy, 1869), *Notharctus* (Leidy, 1870), *Hemiacodon* (Marsh, 1872), *Washakius* (Leidy, 1873), and *Anaptomorphus* (Cope, 1882) (transferred to *Tetoniux* by Matthew, 1914) from North America were all recognized as primates by the early 1880s, and the similarities of *Notharctus* (Leidy, 1873; Wortman, 1903–1904) and *Omomyx* (Wortman, 1903–1904) to South American monkeys were noted in the early 20th century. *Microchoerus* (Wood, 1846), *Adapis* (Cuvier, 1821), and *Necrolemur* from Europe were all recognized as primates by 1873 (*Microchoerus*, Filhol, 1873; Schlosser, 1887; *Adapis*, Delfortrie, 1873; Filhol, 1873; Gervais, 1872), and Lydekker suggested them as possible ancestors of catarrhines in 1885.

Second, if parallelism reflected common underlying trends or orthogenetic tendencies, then these trends could be used to group organisms together. Thus, paradoxically, it was possible to argue that features that had

evolved in parallel in two groups could also be cited as evidence for the groups' close affinities. This paradox is apparent in early debates surrounding the relationship of anthropoids to *Tarsius*. Students of primate morphology had long noted the presence of anthropoid-like features in *Tarsius*, often classifying this genus as a third suborder of primates intermediate between the Lemuroidea and Anthroidea ("Tarsides" of Gervais, 1854; "Tarsii" of Gadow, 1898, in Wood Jones, 1929). Based on the evidence of placentation, Hubrecht claimed that the Order Primates should be restricted to anthropoids, *Tarsius*, and *Anaptomorphus* (i.e., *Tetonius*) *homunculus* (Hubrecht, 1896, 1897a, 1897b, 1897c). In response, Charles Earle, an Osborn-hired curator of fossils at the American Museum of Natural History (AMNH) (Rainger, 1991), argued that osteological features showed that *Tarsius* is closer to lemurs than to anthropoids and should therefore be classified as a lemuroid (Earle, 1897a, 1897b, 1897c). In support of this argument, he pointed out that the only osteological feature linking *Tarsius* to anthropoids—the postorbital septum—was not present in *Anaptomorphus* (i.e., *Tetonius*) and must therefore have evolved convergently in the two groups. However, he also insisted that lemurs should be classified with anthropoids as Primates precisely because one lemuroid, *Tarsius*, had a postorbital septum resembling that of anthropoids (Earle, 1897a)! Thus, Earle argued that a convergent feature could be evidence of close affinity and that parallelism is the expression of inherent and inherited innate tendencies.

Similar logic, but invoking neo-Lamarckian inherited effects of use and disuse, lay behind the definition of Anthroidea provided by Jacob L. Wortman, later Osborn's personal assistant (Rainger, 1991). Wortman agreed with Hubrecht that placental features linked *Tarsius* more closely to anthropoids than to lemurs; however, he also agreed with Earle that osteology, not soft-tissue morphology, should be the basis of classification. He argued that the osteological evidence indicated an origin for South American monkeys from *Notharctus*- or *Omomys*-like forms, and an origin for *Tarsius* from fossil forms such as *Anaptomorphus* (i.e., *Tetonius*). He defined the suborder Anthroidea as follows: "Limbs elongate, extremities prehensile, and fully adapted to an arboreal life; incisors and canines normal in form and position; entocarotid traversing petrotympanic; malar and lachrymal not in contact on anterior rim of orbit; fourth digit of manus shorter than third; three superfamilies or groups, Arctopithecini, Paleopithecini, and Neopithecini" (Wortman, 1903, p. 173).

Wortman revived the Arctopithecini of Huxley (1863) for callitrichids, erected the Neopithecini for adapids and all non-callitrichid anthropoids, and created the Paleopithecini to receive *Tarsius* and its fossil allies, the Anaptomorphidae. He believed that it was impossible to discern the relationships among these groups with certainty, although he did think that these three main branches divided early in anthropoid evolution. Of course, this conclusion required that callitrichids evolved their anthropoid features independently and in parallel with other anthropoids, and that tarsier–anthropoid similarities not present in early Paleopithecini must also have evolved in parallel. However, the common belief among paleontologists in the pervasiveness of evolutionary parallelism made this conclusion palatable.

Third, Mivart and Osborn's belief in pervasive parallelism explained apparent evolutionary trends with reference to innate features of organisms, eventually allowing the definition of higher taxa in terms of the "tendencies" within their constituent lineages. In an intellectual milieu that assumes parallel evolution to be pervasive, and directed by either innate evolutionary tendencies or inheritance of the effects of use and disuse, it is hardly surprising that the first explanations in primatology were permeated with innate tendencies and trends. These explanations, which appeared in the first decades of the 20th century at the hands of Grafton Elliot Smith and F. Wood Jones, explained primate evolution and diversification as the logical extension of the trends that distinguished primates from other mammals: plasticity of behavior and an ability to learn (Smith), and a tendency to transfer weight to the hindlimbs, leading to emancipation of the forelimb (Wood Jones).

The most important result of this common belief in orthogenetic trends, and its associated assumption of widespread parallelism, was its influence on the works of Wilfred E. Le Gros Clark, the founder of modern primatology (Cartmill, 1982). Le Gros Clark's early belief in innate evolutionary tendencies can be traced directly to Osborn. In *Early Forerunners of Man* (1934), Le Gros Clark quotes Osborn's aphorism, "the same results appear independently in descendants of the same ancestors," before characterizing all of evolution as Orthogenesis.

This principle embodies the conception that evolution is the manifestation of an inherent tendency in the germ-plasm to vary along definite and limited lines; the modification of an organism is not due to the natural selection of apparently fortuitous variations which may occur in any direction,

but rather to a process of continuous change which is taking place in the germ-plasm itself (Le Gros Clark, 1934, p. 287).

Le Gros Clark then claimed that the basal stock of the primate order was differentiated from its contemporaries by “evolutionary tendencies (which became successively manifested during the Tertiary epoch)” (1934, p. 282), tendencies that provided “a convenient basis for a definition of the Order” (1934, p. 282). From this basal stock, Le Gros Clark envisaged the derivation of Protolemuroid and Prototarsioid stocks, the former markedly and rapidly specializing in the direction of lemuroids and lorisooids, the Prototarsioid stock avoiding the “deviating tendencies for specialization” by retaining a more primitive body structure, while incorporating tendencies to “progressive development of the brain, skull, teeth, limbs, rhinarium etc.” (1934, p. 285). One group of tarsioids expressing these trends became anthropoids, and those anthropoids that did not branch off the “central stem in which a progressive expansion of the brain has been accompanied by the retention of a bodily structure of a remarkably generalized type” eventually evolved into humans (1934, p. 286). Those lineages that lost the primitive adaptability specialized and evolved in radiations of lemurs, lorises, tarsiers, and nonhuman anthropoids. Members of some of these radiations survived until the present, yielding a series of grades of living primates, paralleling the series of fossil forms.

Anthropoids were central to Le Gros Clark’s scheme. Whereas some of the trends defining the primate order are not found in lemurs, all are present in anthropoids. This is revealed by a comparison of the trends in the skull that he claims define the order as a whole,

progressive reduction of the facial part of the skull, with recession of the snout region and restriction of the nasal cavities—expansion of the neurocranium—forward rotation of the orbital apertures—completion of a postorbital bar—participation of the ethmoid in the medial wall of the orbit (except in the Lemuriformes)—displacement of the foramen magnum towards the base of the skull—formation of an osseous floor of the tympanic cavity from a process of the petrosal bone (Le Gros Clark, 1934, pp. 283–284).

with those of the skull claimed to define Anthroidea:

progressive reduction of the snout region accompanied by a restriction of the nasal cavities—flexion of the basicranial axis and displacement of the facial skeleton below the front part of the neurocranium—great

expansion of the neurocranium—complete rotation forwards of the orbital apertures—enlargement of the entocarotid artery—participation of the ethmoid in the medial wall of the orbit—separation of the orbit from the temporal fossa by the expanded alisphenoid—ectotympanic forming a tubular auditory meatus and disappearance of the bulla as a prominent swelling (except in the Platyrrhines)—expansion of the frontal bones—displacement of the foramen magnum on to the base of the skull (Le Gros Clark 1934, pp. 272–273).

According to these two lists, the trends of the skull distinguishing anthropoids from prosimians are (paraphrased from Le Gros Clark, 1934):

1. flexion of the basicranial axis and displacement of the facial skeleton below the front part of the neurocranium;
2. great expansion of the neurocranium; complete rotation forward of the orbital apertures;
3. enlargement of the entocarotid (internal carotid) artery;
4. separation of the orbit from the temporal fossa by the expanded alisphenoid;
5. ectotympanic forming a tubular auditory meatus (except in platyrrhines);
6. disappearance of the bulla as a prominent swelling (except in the platyrrhines); and
7. expansion of the frontal bones.

Excluding features also found in *Tarsius* (basicranial flexion, facial kyphosis, participation of the alisphenoid in the posterior wall of the orbit, and a tubular external auditory meatus), the trends in the skull distinguishing anthropoids from other primates are those leading toward more forward rotation of the orbital apertures, greater enlargement of the brain, and expansion of the frontal bones.

Le Gros Clark's (1934) explanations of these trends initially consisted of claims that they were orthogenetic, inherent, and innate, but by the time the second edition of *A History of the Primates* (1954) and the first edition of *The Antecedents of Man* (1959) were published, Le Gros Clark had explicitly rejected orthogenesis as an explanation for these trends (Le Gros Clark, 1959, p. 1). This rejection undoubtedly stems from the percolation of the neo-Darwinian synthesis into primatology (Fleagle and Jungers, 1982, p. 204), facilitated by one of the architects of this synthesis, George Gaylord Simpson. Simpson (1944) reconciled observations of apparent orthogenetic phenomena with the microevolutionary mechanisms of population genetics, enabling Le Gros Clark to continue to

interpret primate evolution in terms of trends, but with the driving force behind these trends being natural selection rather than orthogenesis. However, Le Gros Clark continued to view anthropoid origins and evolution as the expression of pervasive primate trends and he never specified what selective forces might account for the divergence of anthropoids from other primates.

“INTENTIONAL VAGUENESS”

As one of the architects of the New Synthesis, the paleontologist, George Gaylord Simpson (1944, 1949) hypothesized that undeviating trends observed in the fossil record were either illusory or susceptible to alternate explanations cast in the framework of adaptation. Moreover, he asserted that macroevolutionary events such as the origins of higher taxa could in theory also be explained with reference to natural selection. He envisaged the origins of a higher taxon as the result of a population of animals invading a new adaptive zone or geographical region, then radiating into “a multiplicity of highly varied, markedly variable, but still rather similar groups” (1949, p. 93). This phase is followed by a process of “weeding out,” whereby dominant groups are favored and other variants are eliminated, resulting in a reduction “to a much smaller number of much more sharply distinct adaptive types, each of which tends to specialize in some particular way of life” (1949, p. 94).

Simpson (1961, p. 212ff) viewed all of primate evolution in this light, eschewing the characterization of primate evolution as an ascending scale of stages from prosimians, through ceboids and cercopithecoids, to hominoids. He envisaged primate evolution beginning with a diverse early Euramerican radiation of Paleocene and Eocene prosimians. The majority of these subsequently became extinct; some survived to radiate in the “asylum” of Madagascar, some specialized into tarsiers, some invaded South America to evolve into and radiate as ceboids, and two lineages entered Africa and evolved separately into cercopithecoids and hominoids.

Like Osborn, Simpson thought that parallel evolution was extremely common (“In the most restricted sense virtually all evolution involves parallelism” [Simpson, 1945, p. 9]), although he rejected orthogenesis as the mechanism to explain it (Simpson, 1949). Rather, parallelism for Simpson was due to natural selection, laws of relative growth, the tendency for groups of common origin to inherit similar habitats and environments, and the fact that “homologous genes tend to mutate in the same way” (Simpson, 1945, p. 9).

Due to this propensity for parallelism in evolution, Simpson allowed what now would be regarded as polyphyletic taxa in his classificatory schemata:

Given a group that is composed of related animals and defined by morphological and related data, the most practical and, at least for the present, the most desirable additional requirement seems to be not that it should be derived from one immediately antecedent genus or species, but, with intentional vagueness, that its immediate ancestry should be included within a group of lower rank than itself (Simpson, 1945, p. 17).

One of the most important components of evolutionary classification was Simpson's incorporation of notions of evolutionary grade. Animals sharing enough features so as to define a distinct level of organization constituted an evolutionary grade (J. Huxley, 1958; Simpson, 1961). Simpson did not discriminate between cases in which the defining features of the grade were present in the last common ancestor of the taxa in the grade, or whether those features evolved in parallel. Indeed, by definition, parallelism only occurs in closely related lineages, and closely related lineages sharing features in common can, under Simpson's definitions, be monophyletic.

Like Mivart and Le Gros Clark, Simpson initially saw his higher taxon Anthroidea as polyphyletic *sensu lato* (Simpson, 1945, 1949), with cercopithecoids, hominoids, and ceboids arising from separate groups of prosimians (Simpson, 1949, figure 17, p. 91). Later, Simpson came to see Anthroidea as monophyletic in his sense in that they were derived "through one or more lineages ... from one immediately ancestral taxon of the same or lower rank" (Simpson, 1961, p. 124). His diagram of these relationships suggests monophyly in a modern sense as well, with hominoids, New and Old World simians all sharing a common stem sprouting from the Eocene prosimian radiation (Simpson, 1961, figure 29, p. 213). However, despite their close phylogenetic relatedness (i.e., monophyly), Simpson saw Anthroidea as a grade because ceboids, cercopithecoids, and hominoids all evolved the same adaptive features separately.

For Simpson, higher taxa like Anthroidea were "either made consistent with a reconstruction of phylogeny or with phylogenetic processes likely to have produced an observable result—or both, for those approaches are closely and often inseparably related. In any case, the taxa reflect evolutionary factors involved in their origin and development ..." (Simpson, 1961, p. 221). Simpson identified "the most significant evolutionary factor in this connection" as adaptation (Simpson, 1961, p. 221). Adaptive explanations, therefore, lie at the heart of the Simpsonian endeavor to characterize and define higher

taxonomic groups: the adaptive significance of the distinctive features of such a group constitutes the explanation for the divergence of that group from its predecessors and for its subsequent adaptive radiation. In an ironic return to the (albeit updated) essentialism characteristic of early biological classification, the search for the defining characteristics of a taxon constituted a search for the “basic adaptation” characterizing the basal members of the higher taxon (whether they be in one or more lineages).

Simpson’s treatment of Anthroidea represented a significant advance over Le Gros Clark’s in two respects. First, he abandoned the attempt to explain all of primate evolution with reference to a single set of evolutionary trends. Each radiation was characterized by its own distinctive features, and the explanations for the existence of these features necessarily differed from one radiation to another. Second, he emphasized the role of natural selection and the process of adaptation as the causal mechanisms responsible for the origin and diversification of higher taxa. Although Simpson did not specify the selective forces that drove the origins of the primate adaptive radiations, his contribution to modern primatology in general, and the study of anthropoid origins in particular, cannot be overstated. Adaptive or functional explanation is one of the two foci of research in primatology today, the other being phylogeny reconstruction.

PHYLOGENETIC HYPOTHESES: FROM VAGUENESS TO PRECISION

Four groups of phylogenetic issues still bedevil investigations of anthropoid origins (Kay et al., 1997, Chapter 5, this volume; Ross et al., 1998). (a) Is Anthroidea a monophyletic group, and what are its synapomorphic features? (b) To which group of fossil or extant primates is Anthroidea most closely related? (c) How do Asian Eocene taxa (Eosimiidae and Amphipithecidae) relate to Anthroidea? (d) How do Eocene and Oligocene anthropoids of Africa (Parapithecidae, Propliopithecidae, Oligopithecidae) relate to the Platyrrhini and Catarrhini?

Is Anthroidea a Monophyletic Group, and What are its Synapomorphic Features?

Evolutionary Biology of the New World Monkeys and Continental Drift (Ciochon and Chiarelli, 1980), the first volume dedicated to the study of anthropoid origins, documents the demise of the anthropoid polyphyly

hypothesis in favor of the hypothesis of anthropoid monophyly. Acceptance of the notion of anthropoid monophyly is partly attributable to mounting evidence from various sources—placentation and fetal membranes (Lockett, 1975, 1980), microcomplement fixation (Sarich and Cronin, 1976), immunodiffusion studies and protein amino acid sequences (Baba et al., 1980; Goodman, 1975, 1976), enamel microstructure (Gantt, 1980), sulcal patterns on the brain (Falk, 1980), postcranial anatomy (Ford, 1980), cephalic arterial patterns (Bugge, 1980), sperm morphology (Martin and Gould, 1980), and the anatomy of the visual system (Cartmill, 1980)—that all pointed toward anthropoid monophyly. Although primate systematists were beginning to abandon pervasive parallelism in favor of cladistics and parsimony, they used cladistic terminology to describe their preferred hypotheses of anthropoid relationships long before they used parsimony analyses to discover them (e.g., Cartmill and Kay, 1978; Lockett, 1975; MacPhee and Cartmill, 1986). Thus, the acceptance of anthropoid monophyly at the beginning of the 1980s preceded the first large-scale phylogenetic analysis of early anthropoid relationships using parsimony (Fleagle and Kay, 1987) (for a small-scale analysis exception, see Baba et al., 1980), and anthropoid polyphyly merely collapsed under the weight of the accumulating evidence.

Just as important for the acceptance of anthropoid monophyly was the influence of theories of continental drift (Tarling, 1980). Prior to continental drift, an Atlantic crossing was implausible, a North American origin for platyrrhines was generally accepted (Gazin, 1958; Gingerich, 1973; Matthew, 1915; Simons, 1972, 1976; Stirton, 1951), and the absence of fossil anthropoids in the early Tertiary deposits of North America suggested that platyrrhines must have evolved their anthropoid features independently of catarrhines. Continental drift made it plausible for platyrrhines to have crossed the Atlantic from Africa to South America during the early Tertiary, after the derivation of the anthropoid stem lineage, but when the two continents were closer together.

The fossil record of early anthropoid evolution did not play much of a role in the acceptance of anthropoid monophyly. Elwyn Simons' fossil discoveries in the Fayum of Africa had revealed an extensive radiation of Oligocene Parapithecidae, which Simons originally (1967) likened to platyrrhines, but he later (Simons, 1972; see also Kay, 1977) came to regard parapithecids as ancestral cercopithecids. Thus, except for Hoffstetter (1980), who proposed that parapithecids were actually basal platyrrhines, the Fayum fossils were not interpreted as providing support for anthropoid monophyly as soon as they might have been.

Thus, mounting comparative evidence from diverse sources identified numerous similarities between platyrrhines and catarrhines that must have evolved in parallel if anthropoids were diphyletic. The diffusion of continental drift into primatology provided a mechanism whereby the disjunct distribution of the catarrhines and platyrrhines could be explained. Anthropoids came to be regarded as monophyletic primarily because of advances in geological theory and comparative analyses, and not because of the application of new methods of phylogeny reconstruction or new fossil discoveries. Recent parsimony analyses have simply corroborated the assumption of anthropoid monophyly (Kay et al., 1997, Ross et al., 1998)

To which Group of Fossil or Extant Primates is Anthroidea most Closely Related?

Although the adoption of cladistic methods by paleoprimatologists did not resolve for everyone the problems of basal primate cladogenesis debated by Earle and Hubrecht at the end of the 19th century, it did make such hypotheses more precise and open the way to a more rigorous analysis of character evolution. In the mid-1980s, the general acceptance of anthropoid monophyly caused debate to become focused on the question of whether tarsiers are more closely related to Anthroidea than to Strepsirrhini, and the separate, but related question (Rasmussen, 1986) of which non-anthropoid fossil group is most likely to have given rise to Anthroidea. Three hypotheses attracted supporters (MacPhee and Cartmill, 1986): the lemurphile hypothesis that some lineage of cercamoniine or notharctine adapiform gave rise to anthropoids (e.g., Gingerich, 1980); the omomyophile hypothesis that anthropoids and tarsiers evolved from separate lineages of omomyiforms (Rosenberger, 1986; Szalay, 1975a; Szalay and Delson, 1979; Szalay et al., 1987); and the tarsiphile hypothesis that anthropoids and tarsiers share a common ancestor more recently than either does with either omomyiforms or adapiforms (Cartmill and Kay, 1978; Cartmill et al., 1981; MacPhee and Cartmill, 1986).

The lemurphile hypothesis, that anthropoids arose from a lineage of fossil adapids was originally proposed by Wortman (1903). Gingerich (1980), Rasmussen (1990), Franzen (1987, 1994), and Shoshani et al. (1996, appendix 1) advocate various versions of the adapid–anthropoid hypothesis. Simons and Rasmussen (1996) provide the most explicit recent presentation of the evidence for an adapid–anthropoid clade. They have even gone so far as to

resurrect Wortman's classification (Simons and Rasmussen, 1996, p. 285). Their evidence has been reviewed in detail by Ross et al. (1998), who give reasons for rejecting with it. More recent phylogenetic analyses by Gunnell and Miller (2001, figure 8, p. 188) and Seiffert et al. (Chapter 7 this volume) likewise do not find support for an adapid–anthropoid clade.

The omomyophile hypothesis advocates separate origins for *Tarsius* and Anthropoidea among different groups of omomyids (Beard et al., 1998; Rosenberger, 1986; Szalay, 1975a, 1975b; Szalay et al., 1979, 1987). Various omomyids have been advanced as anthropoid ancestors, including *Teilhardina*, *Omomyys*, or *Chumashius* (Cartmill and Kay, 1978; Hofstetter, 1980; Kay, 1980; Rose et al., 1994; Rosenberger, 1986; Szalay, 1976; Szalay and Delson, 1979). Discovery of skulls of the washakiine omomyid, *Shoshonius cooperi*, from late early Eocene (50.5 million years ago [Ma]) localities in Wyoming led Beard et al. (1991) to hypothesize that *Tarsius* is more closely related to *Shoshonius* than to other omomyids or anthropoids.

By 1994, when the edited volume on *Anthropoid Origins* was published (Fleagle and Kay, 1994a), these workers still held their disparate positions (Franzen, 1994; Kay and Williams, 1994; Rasmussen, 1994; Ross, 1994). The application of cladistic techniques to the problems surrounding primate higher taxonomic relationships did provide some support for the tarsiphile hypothesis, but the answer was by no means definitive (Kay et al., 1997; Ross et al., 1998; Shoshani et al., 1996).

That cladistic parsimony has not resolved these issues to everyone's satisfaction is attributable to personal as well as scientific factors. Amongst the latter, a poor fossil record and long branch lengths for crucial taxa, such as *Tarsius* are most important. The branch-length problem in particular will make it difficult to resolve the relationships among extant primates, even by analysis of the massive molecular data sets on mammal relationships now available (e.g., Eizirik, Chapter 2 this volume; Murphy et al., 2001), although the analysis of retropositions of short interspersed nuclear elements (SINE) markers appears to offer more promise (Schmitz, 2001, Chapter 3 this volume). The only way to shorten the branch lengths of the extant primate clades is to discover new fossils; this fact suggests that *both* molecular and morphological data will be needed to resolve the question of basal primate cladogenesis.

The extension of the record of definitive anthropoids back into the late Eocene of Africa (Kappelman et al., 1992; Simons and Rasmussen, 1994), the discovery of possible basal anthropoids and tarsiers in the middle Eocene of

Asia (Beard et al., 1994, 1996; Ducrocq, 1999; Jaeger et al., 1999), and the suggestion that primates might have been distinct in the Cretaceous (Martin, 1993), have raised the possibility that the anthropoid stem lineage (Beard and MacPhee, 1994; Culotta, 1992; Fleagle and Kay, 1994b; Godinot, 1994), or the common lineage of tarsiers and anthropoids (Ross, 2000), branched off prior to the diversification of omomyiforms and adapiforms in the early Eocene. If true, this eliminates most of the primate Tertiary fossil record of North America and Europe from relevance for resolving questions about the ancestry of Anthropoidea; it suggests a fundamental dichotomy between omomyids and adapids of the Northern continents and Anthropoidea of Africa and South America (Fleagle and Kay, 1994b), and focuses our attention on early-middle Eocene fossils from Africa, Asia, and South America (Ross, 2003).

Are there Asian Eocene Anthropoids?

This brings us to a key area of debate—the phylogenetic status of various Asian Eocene primates—*Pondaungia*, *Amphipithecus*, *Myanmarpithecus*, *Siamopithecus*, *Eosimias*, and *Babinia*.¹ Over the past 10 years, the phyletic position of these taxa has come under increased scrutiny. The first of these taxa to be described were *Pondaungia* (Pilgrim, 1927) and *Amphipithecus* (Colbert, 1937), each known from just a few poorly preserved jaws and cheek teeth. The relationships of these taxa was hotly debated (Simons, 1972; Szalay, 1970) with no consensus being achieved. In the late 1970s, the two were not considered closely related to one another. Szalay and Delson (1979) placed *Amphipithecus* among the Adapidae and relegated *Pondaungia* with query to catarrhine primates. A few additional specimens that accumulated in the 1980s (Ba Maw et al., 1979; Ciochon et al., 1985) were interpreted as being anthropoids. In 1994, two papers (Ciochon and Holroyd, 1994; Godinot, 1994) made the important recognition that *Amphipithecus* and *Pondaungia* were closely related taxa within a group now called Amphipithecidae (see Holroyd et al., 2002; Shigehara et al., 2002). Ciochon abandoned the notion that these taxa were anthropoids and allocated both to the Adapidae, while Godinot briefly continued to regard them as Anthropoidea but subsequently also settled on an allocation to Adapidae (Godinot, 1998). Recovery of much better material of *Amphipithecus* and *Pondaungia* (Chaimanee et al., 2000; Ciochon et al., 2001; Gunnell et al., 2002;

¹ Another south Asian taxon, *Wailekia*, proposed to have anthropoid affinities in probably a primitive sivaladapine adapid (Tao and Beard, 1998).

Jaeger et al., 1998; Shigehara et al., 2002) and the description of the taxa *Myanmarpithecus* (Takai et al., 2001) and *Siamopithecus* (Chaimanee et al., 1997; Ducrocq, 1998, 1999; Ducrocq et al., 1995) has fueled the debate about whether amphipithecids are adapids or anthropoids.

With the discovery of *Eosimias* in China, a more compelling candidate for the existence of an Eocene Asian anthropoid has emerged. Beard and colleagues have made a strong case for its anthropoid affinities from dental and postcranial remains (Beard et al., 1994, 1996; Dagosto et al., 1996, 2000). The identification of a small omomyid-like isolated petrosal bone as belonging to *Eosimias* (MacPhee et al., 1995) presents some challenges to the anthropoid status of this taxon but we do not accept this allocation (Ross and Covert, 2000; Ross et al., 1998). The facial and dental remains of a somewhat larger eosimiid called *Bahinia* from Myanmar (Jaeger et al., 1999) support its attribution to eosimiids and support the allocation of the group to basal Anthroidea (Beard, 2002; Jaeger et al., 1999; Kay et al., Chapter 5, this volume).

Origins of Crown Anthropoids

Debate concerning cladogenesis within early anthropoids centers around the phyletic positions of the Oligopithecidae and Parapithecidae (and some would say Amphipithecidae) relative to platyrrhines and catarrhines. Late Eocene anthropoids are best preserved and most abundant in several Egyptian localities. Two principal groups—Propliopithecidae and Parapithecidae—are universally recognized. Propliopithecids include *Propliopithecus* and *Aegyptopithecus*; a core parapithecid group containing *Apidium*, *Parapithecus*, and *Simonsius* (regarded by many as a species of *Parapithecus*) is accepted by most workers, (e.g., Beard, 2002; Fleagle et al., 1987; Gunnell et al., 2001; Kay et al., 1994a; Simons, 1974; Simons et al., 1994). Placements of other taxa are more controversial.

Oligopithecidae (*Oligopithecus*, *Catopithecus* late Eocene, Africa) are considered by Rasmussen and Simons (Rasmussen and Simons, 1988; Simons, 1989, 1990; Simons et al., 1989) to be primitive members of the Propliopithecidae, “true catarrhines that are plausibly ancestral to later hominoids and cercopithecoids” (Simons et al., 1994). Others have also argued that *Oligopithecus* is a stem catarrhine (Kay, 1977; Simons, 1972; Szalay et al., 1979) or a stem anthropoid (Hofstetter, 1980). At the opposite extreme, Gingerich (1980) argued that *Oligopithecus* is very similar dentally to some Adapidae and may even be an adapid.

The Parapithecidae have been argued to be near the ancestry of Old World monkeys (Cercopithecidae) and *Oreopithecus* (Gregory, 1922; Kay, 1977,

Simons, 1960, 1974), to New World monkeys (Hofstetter, 1980), or the sister group of all other living and fossil anthropoids (Fleagle et al., 1987; Harrison, 1987; Hofstetter, 1977, 1980; Simons et al., 1994). *Qatrania*, *Serapia*, and *Arsinoea* of the late Eocene are placed by some individually or collectively among the Parapithecidae while others regard them as uncertain affinities.

The history of placement of *Proteopithecus sylviae* is even more vexed. Some regarded it as a separate family possibly related to platyrrhines (Kay and Williams 1994; Simons, 1997; Takai et al., 2000), while others placed *Proteopithecus* with *Oligopithecus* and *Catopithecus* as basal anthropoids (Kay et al., 1997; Ross et al., 1998). Since 1998, publication of additional postcranial, cranial, and dental material of *Proteopithecus* and *Catopithecus* have suggested that the former is a basal parapithecid while the latter is a propliopithecid (Seiffert et al., 2000, 2001; Simons and Seiffert, 1999).

ADAPTIVE EXPLANATIONS FOR ANTHROPOID ORIGINS

The first adaptive explanations for the origin of anthropoids preceded the universal acceptance of anthropoid monophyly. They were classically Simpsonian in approach in two ways. First, they were concerned with postulating the selective forces that drove the adaptive shift defining Anthroidea, no matter whether anthropoids were descended from one (Cartmill, 1970) or two (Cachel, 1979a) lineages of non-anthropoids. Second, the explanation for the divergence of Anthroidea from its predecessors and its subsequent adaptive radiation was sought in the adaptive significance of the distinctive features of the group.

Hypotheses regarding the functional and ecological significance of specific features were generated and tested using comparative methods, with the emphasis being on features of the head, such as the postorbital septum, fused mandibular symphysis, and neural enlargement. Explanations were sought that had general applicability across mammals, with comparisons between extant primate and nonprimate mammals being used not only to explain why some prosimian group had evolved into an anthropoid, but why other lineages had not! In addition, the functional principles embodied in the explanations were used, by Cartmill at least, to hypothesize about the group of primates most likely to have given rise to anthropoids.

Cartmill

M. Cartmill initially (1970) posited that anthropoids evolved from tarsier- or *Pseudoloris*-like (Eocene, Europe) prosimians with an apical interorbital

septum and an anteriorly displaced olfactory fossa. When this lineage shifted to “a diurnal and largely herbivorous way of life,” reduction in orbital diameter allowed the braincase to expand forward over the orbits, increasing the degree of orbital frontation (or “verticality” of the orbital margins), resulting in an animal much like a small platyrrhine. Expansion of the anterior portion of the braincase, accompanied by reduction in orbital diameter encouraged the formation of a postorbital septum “to insulate the eyeball, with its increasingly fine-grained diurnal retina, from impulses originating in the muscular and osseous masticatory apparatus filling the temporal fossa” (Cartmill, 1970, p. 412).

Cartmill suggested that a shift to diurnality in Malagasy primates did not result in the evolution of anthropoid-like features because the ancestral Madagascan primate resembled lorises rather than tarsiers in having orbits that converged upward toward the skull roof, rather than rostrally toward the end of the snout. As a result, reduction in relative orbit size in lineages of diurnal Malagasy prosimians did not result in increase in size of the anterior cranial fossa, the gap between postorbital bar and braincase remained large, and a postorbital septum did not, therefore, develop. “As a consequence, masticatory activity continued to interfere with visual precision. Modern diurnal prosimians display a diffuse, cone-rich area centralis (Rohen and Castenholtz, 1967), but, in the absence of a postorbital septum, no fovea has been developed” (Cartmill, 1970, p. 417).

The problem with linking the evolution of a postorbital septum to the presence of a fovea in a lineage of tarsier-like animals is that foveae are rare in nocturnal animals, and extremely rare in animals, like *Tarsius*, with rod-dominated retina (Cartmill, 1980; Walls, 1942; Ross, Chapter 19 this volume). This led Cartmill subsequently to propose a different hypothesis for the evolution of the distinctive anthropoid cranial features (Cartmill, 1980). The absence of a tapetum lucidum and the presence of a retinal fovea in *Tarsius* had suggested to several workers that tarsiers had a diurnal ancestry (Le Gros Clark, 1959; Martin, 1973, 1975, 1979). Cartmill (1980) suggested that this diurnal lineage was also shared with anthropoids, that it consisted of diurnal, predominantly frugivorous animal with *Saimiri*-like foraging habits, including that they visually scanned their environment for insects while chewing their last piece of food, and that it was in this context that the postorbital septum and retinal fovea evolved. To avoid competition with birds, the lineage leading to *Tarsius* then reverted to a nocturnal lifestyle, resulting in the loss of retinal cones, and ocular hypertrophy to compensate for the lack of a tapetum. Unlike tarsiers, the stem lineage of anthropoids managed to maintain a diurnal lifestyle by evolving

a fused mandibular symphysis (Beecher, 1979) and color vision, allowing them to avoid competition with birds by exploiting a diet of unripe fruits.

Cachel

An alternative explanation for the origin of distinctively anthropoid features was presented by S. Cachel (1979a, 1979b). In Cachel's scheme, increasing global seasonality in the late Eocene required increased body size to mitigate internal temperature fluctuations and made fruit resources more predictable, making them a viable dietary resource for large-bodied primates (Cachel, 1979a). Resurrecting Polyak's (1957) thesis that color vision evolved in primates to allow them to find ripe fruit by sight, Cachel suggested that increased body size, diurnality, and frugivory were all interrelated with the evolution of color vision (Cachel, 1979a, p. 356). Emphasis on vision for locating food resources led to the evolution of neurological features distinctive of anthropoids, such as an increased size of the neocortex in general—and of the temporal lobe in particular—and in a reduction in size of the olfactory bulbs.

Cachel also suggested that frugivory “or extensive incisal preparation of food” was causally related to the evolution of the anthropoid postorbital septum (1979b). She suggested that the function of the postorbital septum was to facilitate enlargement of the anterior temporalis muscle by augmenting the area available for its origin, and that this additional anterior temporalis improved the ability to generate vertically directed bite forces at the incisors (Cachel, 1979b, p. 13).

Cachel suggested that non-anthropoid primates do not need a postorbital septum because they do not exert vertically directed bite forces at the incisors. She argued that during “raking of bark,” the strepsirrhine toothcomb experiences anteroventrally directed forces that are resisted by the posterior temporalis. Thus, one might expect the posterior temporalis to be emphasized in strepsirrhines and the anterior temporalis to be emphasized in anthropoids. Cachel argued that the postorbital septum in *Tarsius* evolved “in response to mechanical demands for support of hypertrophied eyes, rather than because of masticatory demands” (Cachel, 1979b, p. 13). Cachel noted that *Tarsius* also lacks the mesiodistally broad incisors seen in anthropoids, suggesting to her that, even if *Tarsius* uses its upper incisors to “stab and immobilize vertebrate and invertebrate prey,” any vertical stresses generated during such activities will be “concentrated in a small mesiodistal span” (Cachel, 1979b, p. 13).

Rosenberger

A. L. Rosenberger's (1986) model resembled Cachel's in suggesting a link between incisor biting and the evolution of a postorbital septum, and resembled Cartmill's in seeing the echoes of an omomyiform ancestry in the anthropoid response to this selective regime.

Rosenberger incorporated the features of the skull distinguishing anthropoids from other primates (fused frontal bones; recession of the face; closure of the orbit by enlargement and fusion of the zygomatic to the braincase; enhanced grinding stroke of the chewing cycle; fusion of the mandibular symphysis; enlargement of the incisors and their transverse alignment in the tooth-row; blunting of the premolars; and cancellous petrosal bones) into a functional hypothesis explaining their interrelated evolution (Rosenberger, 1986). He suggested that the highly reduced interorbital region of anthropoids reduces the skull's ability to resist twisting of the face on the braincase during mastication and incision, requiring a laterally positioned postorbital septum to resist these stresses. The postorbital septum "braces the facial skull against twisting produced by the system and reinforces the origin of the masseter muscle against enlarged forces" (Rosenberger, 1986, p. 79). The trabeculated anterior accessory cavity of the anthropoid middle ear, Rosenberger argued, insulates the hearing apparatus from vibrations conducted by the "heavily sutured and braced anthropoid skull." He concluded by observing that many of these features claimed to be distinctive of anthropoids—such as the short, recessed face, reduced nasal cavity, and narrow interorbitum—are also found among other "haplorhines" (i.e., omomyiforms), and that such animals are the most likely candidates for anthropoid ancestry (Rosenberger, 1986; Szalay et al., 1987).

Ross

In their attempts to explain the origin of anthropoids Cartmill, Cachel, and Rosenberger had been drawn to explanations for the origin of the postorbital septum. As one of the most unusual features of the anthropoid skull, the clues to the distinctive selective forces that drove the divergence of anthropoids from other primates were reasonably sought in a distinctive structure. Continuing this approach, Cartmill's student, C. F. Ross, centered his explanation for anthropoid origins on a functional analysis of the postorbital septum.

Cachel's hypothesis linking the presence of the postorbital septum to incisal preparation of hard fruits had been rendered less compelling by observations

that in most platyrrhines only a small part of the postorbital septum gives origin to anterior temporalis (Ross, 1995a), and that the anterior temporalis of macaques, humans (Hylander and Johnson, 1985), and owl monkeys (Ross and Hylander, 2000) is not unusually utilized during incision. Nor were some elements of Rosenberger's hypothesis supported by the experimental data. In vivo bone strain data suggested that the postorbital septum is not likely to have evolved from a postorbital bar in order to decrease stresses in the lateral orbital wall engendered during mastication and incision (Ross and Hylander, 1996), and the twisting of the face hypothesized to obtain in primates (Greaves, 1985; Rosenberger, 1986) was not found in macaques (Hylander et al., 1991) or owl monkeys (Ross and Hylander, 1996), leading these authors to reject the suggestion that this is an important loading regime in anthropoids. Although subsequent work (Ravosa et al., 2000a, b) has suggested that the face of the strepsirrhine *Otolemur* may twist on the braincase during mastication (Ross, 2001), the low strain magnitudes observed during twisting do not suggest that this is a particularly stressful loading regime (Ravosa et al., 2000a, b).

Ross argued that the functional significance of the postorbital septum lay elsewhere. Noting that anthropoids have both highly frontated and convergent orbits (Ross, 1995b; see also Cartmill, 1970), he suggested that this unusual orbit orientation dragged the anterior temporalis rostrally, impinging on the orbital contents. Were the postorbital septum not present, contractions of temporalis would disturb the visual system. Thus, Ross (1996) agreed with Cartmill that the postorbital septum probably evolved to protect the eye from movements in the temporal fossa. However, rather than seeing increasing visual acuity as the driving force behind evolution of the septum (Cartmill, 1980), Ross suggested that changes in orbit orientation would necessitate the evolution of a septum, even in the absence of enhanced visual acuity.

What then are the causes of the unusually vertical and convergent orbits of anthropoids? Ross (1995b, 1996) posited that a shift to diurnality at small body size would result in (a) high orbital convergence through the allometric consequences of reduced relative orbit size, and (b) high orbital frontation as a result of increased size of the brain—especially the frontal lobes—pushing the superior orbital margin rostrally, or rotating the face down relative to the neurocranium as a result of basicranial flexion (Ross and Ravosa, 1993). Thus, many of the features of the anthropoid face could be explained with reference to a shift to diurnality at small body size (Kay et al., 1997; Ross, 1996). A small, nocturnal visual predator, with orbits highly approximated below the olfactory tract, provided

the most likely substrate from which an anthropoid lineage could evolve, leading him to follow Cartmill (1980) and Rosenberger (1986) in suggesting that anthropoids are likely to have evolved from omomyiforms (Ross, 1996). Ross (1995b) suggested that strepsirrhines did not evolve anthropoid-like features when they became diurnal because strepsirrhines likely evolved diurnality at a larger body size than the ancestral anthropoid, with concomitant differences in the allometric effects on orbit orientation.

This model of anthropoid origins was later expanded to incorporate paleontological discoveries and phylogenetic analyses of the late 1990s, as well as functional morphological research on the masticatory apparatus (Ravosa, 1999), the visual system, the locomotor apparatus, and behavioral ecology (Ross, 2000). Phylogenetic analyses using parsimony had provided some support for the notion that tarsiers are the sister taxon of anthropoids, and that omomyiforms are the sister taxon to these crown haplorhines (Kay et al., 1997; Ross et al., 1998; Shoshani et al., 1996). Fossil discoveries in Asia had revealed a radiation of probable basal anthropoids (Eosimiidae, Beard et al., 1994, 1996), tarsiiforms, and haplorhines, weighing in at 100 g, or less (Gebo et al., 2000), and with teeth indicative of insectivory (Ross, 2000), or insectivory/frugivory (Jaeger et al., 1999). Together, these data supported hypotheses that the first members of the anthropoid stem lineage were small, predominantly insectivorous haplorhines (Ross, 1995b, 1996), or frugivore-insectivores (Cartmill, 1980). Studies of the visual systems of extant anthropoids had also revealed them to be characterized by highly convergent orbital margins, possibly small corneas relative to axial length of the eye, a retinal fovea with high concentrations of photoreceptors and ganglion cells, and extreme magnification of the foveal and parafoveal regions of the visual field in the visual cortex. Ross (2000) concluded that at least anthropoid origins, and possibly the divergence of the tarsier–anthropoid stem lineage, was accompanied by a shift from nocturnal to diurnal visual predation on insects at small body size (<100g). These early anthropoids had small brains, unfused mandibular symphyses, and either dichromatic or trichromatic vision. The relatively large brains—and fused mandibular symphyses of crown anthropoids—and the trichromacy seen in some of them, evolved later in anthropoid evolution.

Hylander and Ravosa

Beginning in the mid-1970s, W. L. Hylander's studies of primate jaw function had yielded important insights into the functional significance of one of the hallmarks of extant anthropoids: the fused mandibular symphysis. In vivo

studies of galagos, macaques, baboons, and owl monkeys had demonstrated that the balancing side jaw adductors of anthropoids are recruited much more than the balancing side jaw adductors of galagos, leading to the hypothesis that “symphyseal fusion is an adaptation to strengthen the symphysis so as to prevent its structural failure due to increased stresses associated with increased recruitment of balancing-side muscle force” (Hylander et al., 2000). Hylander’s work had also demonstrated that anthropoids evince a characteristic “wishboning” of jaw loading during the power stroke of mastication, due in part to late activity of the balancing-side deep masseter muscle, a muscle recruitment pattern not seen in galagos (Hylander et al., 2000).

Ravosa (1999; Ravosa et al., 2000; Ravosa and Hogue, Chapter 17 this volume) incorporated these results into a model of the early evolution of the masticatory apparatus in stem anthropoids, based on a phylogeny of anthropoid relationships suggested by Kay et al. (1997; Ross et al., 1998). Ravosa argued that the increasing body size during early anthropoid evolution predicted by the phylogeny was probably associated with increased mastication of tougher foods, including obdurate fruits and leaves. This would have required increased recruitment of balancing-side jaw-adductor muscles, with a concomitant increase in degree of symphyseal fusion to counter increased stresses associated with dorsoventral shear (Ravosa, 1999). In addition, anthropoids also exhibit increased height of the ramus of the mandible, (possibly due to increased facial kyphosis and basicranial flexion), resulting in a more vertically oriented line of action for the superficial masseter muscle. This in turn would have decreased the ability of this muscle to effect mediolateral movements of the mandible during mastication, necessitating the recruitment of the deep masseter late in the power stroke to fill this role (Ravosa et al., 2000). Increased recruitment of balancing-side deep masseter during the power stroke may also have functioned to increase the amount of transverse movement and occlusal force in anthropoid evolution (Ravosa et al., 2000).

Function and Phylogeny in Anthropoid Evolution

In these scenarios, the explanations for anthropoid origins and early evolution inhere in functional explanations for the origin of the features that distinguish anthropoids from non-anthropoid primates. These accounts all posit causal relationships between these features, such that acquisition of certain of them is posited to have been, in part, caused by the presence of others. For example, Rosenberger’s explanation posited that the existence of a reduced interorbitum

and a fused mandibular symphysis resulted in a pattern of stresses in the facial skull that necessitated the presence of a postorbital septum. The absence of symphyseal fusion in basal anthropoids, which have septa, effectively falsifies this hypothesis. Ross hypothesized that increased orbital frontation and convergence necessitated the presence of a postorbital septum to protect the orbital contents; the level of frontation in *Simonsius grangeri* is relevant to this hypothesis (Simons, Chapter 8, this volume). Ravosa argued that increased facial kyphosis produced increased verticality of the superficial masseter, which in turn necessitated the use of the deep masseters to produce transverse forces during the power stroke of mastication.

These explanations are distinguished from those of Elliot Smith, Wood Jones, and Le Gros Clark in abandoning references to a monolithic set of innate orthogenetic tendencies pervading the primate order. Instead, they hypothesize that the distinctive anthropoid features evolved in response to selection for their ability to perform certain functions, and these selective forces are different from those responsible for the origins of the distinctive attributes of primates or hominids.

Thus, post-Simpsonian explanations differ from those of Le Gros Clark and his predecessors in dividing primate history into separate evolutionary episodes, each requiring its own unique functional/adaptive explanation. The chronological order of events is seen as important because the way that a shift is achieved is thought to be strongly influenced by the historical context in which it occurs (e.g., Szalay, 1984). Modern phylogeny reconstruction, with its precise phylogenetic branching patterns and character-state optimizations, provides the ground-plan on which these functional/adaptive explanations are being built and provide important data to test their validity. The importance of identifying a well-corroborated phylogeny of early anthropoids and their relatives accounts for the robust debate that still persists.

Two uses for these phylogenies and character-state reconstructions are particularly germane for the study of anthropoid origins. First, phylogenetic hypotheses and character-state optimizations are used to *predict* explicit sequences of changes during anthropoid evolution that are then explained using ecological or biomechanical principles (e.g., Ravosa, 1999; Ross, 2000). Second, character-state distributions on phylogenies can also be used to *test* hypotheses regarding the coevolution of certain features during anthropoid evolution, such as color vision and frugivory (e.g., Heesy and Ross, Chapter 24 this volume). Third, both phylogenetic branching information and character-state reconstruction can be used to evaluate attempts to “back-calculate” the phylogenetic and morphological

contexts of the anthropoid adaptive shifts from the morphological consequences characterizing extant and early fossil anthropoids (Cartmill, 1970, 1980; Rosenberger, 1986; Ross, 1996). These “back-calculated” contexts are also vulnerable to falsification by showing that the functional principles on which they are based are erroneous, or by fossil discoveries which reveal character-state combinations that falsify hypotheses based on studies of extant animals (see Ross, 2000 for examples; Lee and Doughty, 1997).

In addition to modern techniques for phylogeny reconstruction and character-state optimization providing the ground-plan on which functional/adaptive explanations are being built, the fossil record is generating the raw material from which these phylogenies are constructed. Although the fossil record is argued above to have played little part in the initial acceptance of the monophyly of crown anthropoids, it is certainly exerting a powerful influence on current studies of anthropoid origins.

The fossil record reveals new taxa with combinations of character states not found in living taxa (e.g., Ross, 2000), drawing into question the causal associations between characters posited on the basis of the study of extant animals. For example, *Catopithecus*, from the Eocene of Africa, lacks the fusion of the mandibular symphysis characteristic of extant platyrrhines and catarrhines, but possesses a postorbital septum, thereby breaking Rosenberger’s hypothesized functional link between symphyseal fusion and possession of the septum. Lack of enlargement of the frontal lobes of the brain in tarsiers and *Simonsius* (Simons, Chapter 8 this volume) contradict hypotheses linking frontal lobe enlargement to postorbital septum origin (Ross, 1996).

New fossil taxa positioned phylogenetically and temporally close to the anthropoid stem lineage also provide the most direct insight into the anatomy and ecology of early anthropoids. Indeed, real animals that actually existed (i.e., fossils) arguably provide a better test of character-state combinations predicted by adaptive hypotheses than do character-state combinations predicted by character optimization on phylogenetic trees. Of course, some characters, such as the type of color vision, will never be recovered from fossils, making some degree of character-state reconstruction necessary (Heesy and Ross, 2001, Chapter 24 this volume).

Anthropoid origins will remain an exciting focus of paleoprimatology for many years to come. New fossils, new phylogenies, and new functional/adaptive analyses are needed as are better methods for integrating these data and using them to enlighten each other.

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